Environ Monit Assess (2024) 196:62
https://doi.org/10.1007/s10661-023-12232-3

RESEARCH

Application of MaxEnt modeling to evaluate the climate change effects on the geographic distribution of *Lippia javanica* (Burm.f.) Spreng in Africa

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Received: 5 February 2023 / Accepted: 7 December 2023 / Published online: 19 December 2023

Abstract *Lippia javanica* is a typical indigenous plant species mostly found in the higher elevation or mountainous regions in southern, central, and eastern Africa. The ongoing utilization of the species for ethnobotanical applications and traditional uses, coupled with the changing climate, increases the risk of a potential reduction in its geographic distribution range in the region. Herein, we utilized the MaxEnt species distribution modelling to build the *L. javanica* distribution models in tropical and subtropical African regions for current and future climates. The MaxEnt models were calibrated and fitted using 286 occurrence records and six environmental variables. Temperatures, including temperature seasonality [Bio 4] and the maximum temperature of the warmest month [Bio 5], were observed to be the most significant determinants of *L. javanica's* distribution. The current projected range for *L. javanica* was estimated to be 2,118,457 km^2. Future model predictions indicated that *L. javanica* may increase its geographic distribution in western areas of the continent and regions around the equator; however, much of the geographic range in southern Africa may shift southwards, causing the species to lose portions of the northern limits of the habitat range. These current findings can help increase the conservation of *L. javanica* and other species and combat localized species loss induced by climate change and human pressure. We also emphasize the importance of more investigations and enhanced surveillance of traditionally used plant species in regions that are acutely susceptible to climate change.

Keywords Africa · Climate change · *Lippia javanica* · Medicinal plants · Niche modeling · Species distribution models

Boniface K. Ngarega and Paul Chaibva contributed equally to this work

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10661-023-12232-3.

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Introduction

Since time immemorial, plants have been the primary source of medicine, and their natural products continue to benefit humankind. Indigenous herbs have been widely utilized as open access according to established practices in rural societies in Africa. Unfortunately, due to overharvesting, this widely tolerated approach exposes these plants to local extinction threats (Dovie et al., 2007). These threats are expected to be further enhanced by other anthropogenically caused environmental changes, particularly global climate change. Therefore, effective conservation management is required to address these threats to maintain these precious natural resources. Reliable and detailed information about a species' spatial distribution is critical for effective conservation planning strategies (Liu et al., 2013).

Lippia javanica (Burm.f.) Spreng (Verbenaceae), which is popular among the indigenous human communities in southern and eastern Africa, has a history of traditional applications as a food ingredient, refreshing beverage or natural herbal tea due to its presumed medicinal and health characteristics (Mokoka, 2007; de Campos et al., 2011; Narzary et al., 2015). Previous ethnobotanical and pharmacological studies, for instance, have reported a broad range of applications of the species, including antiviral, antibacterial, antioxidant, antidiarrheal, anti-inflammatory, antitrypanosomal, and anticonvulsant and repellent activities (Bahlul et al., 2011; Madzimure et al., 2011; Nzira et al., 2009). These effects are arguably contributed to by the essential volatile oils such as myrcene, linalool, and limonene (Chagonda et al., 2000) and other secondary components including carvone, myrcenone, pipentenone, tagetenone, p-cymene, ipsenone, and β-caryophyllene (Dlamini, 2006; Manenzhe et al., 2004; Pretorius, 2010; Wolffe, 2008) that have been documented to occur in abundance at different tissues of *L. javanica*. Furthermore, due to their aromatherapeutic characteristics, the oils found in *L. javanica* have the potential to be economically employed in the pharmaceutical and cosmetics industries. Recently, the reported ability of *L. javanica* to heal colds, coughs, sore throats, and suppress influenza has drawn unwarranted attention to the species as a home-made therapy for suppressing the symptoms of the novel SARS-CoV-2 (Covid-19) virus (Mfengu et al., 2021; Rankoana, 2021; Vroh, 2020). Despite its deceptive species name, the distribution of *L. javanica is* restricted to a continuous range from the East African Rift to the eastern parts of southern Africa. This impressive north–south distribution range reflects the mountain chains' availability and climatic conditions in the eastern parts of tropical to subtropical Africa. In turn, the species' distribution range may enable it to tolerate climatic fluctuation, including the estimated consequences of global climate warming. However, range shifts may considerably impact local communities utilizing the plant species for medicinal practice.

Over the years, conservationists have increasingly applied statistical species distribution models to predict the distributions of various plant species (Mkala et al., 2022; Zhao et al., 2018). These species distribution models (SDMs) approximate the correlation between the ecological habitat of species and the environmental variables and are broadly used in ecology, conservation, and biogeography studies (e.g., Deb et al., 2020; Ngarega et al., 2022; Zhu et al., 2020). Because of the rapid growth of SDM techniques, multiple methods, platforms, and software are now accessible (Mkala et al., 2022; Zhu et al., 2020). Because of the diverse concepts and algorithms, each model has its advantages and limitations, and the performance of each model becomes unstable if the input data is modified (Thuiller et al., 2005). MaxEnt modeling has been used widely for its proven performance with presence only data (Phillips & Dudík, 2008; Elith et al., 2011).

For *L. javanica*, information about the distribution range and ecology is still scarce (Malahlela et al., 2019), yet critical to understanding how climate change and human pressure may influence the species in the African continent. Here in, we examined the potential geographic distribution of *L. javanica* in Africa under current and future climate conditions represented by three shared social-economic pathway scenarios (SSP1–2.6, SSP2–4.5, and SSP5–8.5) using MaxEnt. We aimed to (i) identify the environmental variables influencing the distribution of *L. javanica*, (ii) estimate the current distribution range and (iii) estimate future range size changes of *L. javanica* under different climate scenarios. The research findings will provide new insights into the distribution projection, laying the groundwork for a thorough understanding of the establishment, usage, and management of *L. javanica* and other plant species used for traditional practices in the region.

Materials and methods

Species localities

Species occurrence data for *Lippia javanica* were retrieved from the Global Biodiversity Information Facility (GBIF; https://doi.org/https://doi.org/10.15468/dl.tqpf4q, accessed on April 21, 2022). Locality descriptors and Google Earth™ were employed to georeference occurrence data that lacked geographic coordinates with two-decimal degree accuracy. Collections with localities outside of Africa and accessions with incomplete entries, such as the ones missing both locality descriptions and geographic coordinates, were excluded. After the deletion of duplicate entries, we further improved the dataset to avoid spatial biases by spatial filtering for a 20-km distance between collections using the package "*spThin*" in the R platform (Aiello-Lammens et al., 2015). The 286 occurrence records for *Lippia javanica* were utilized in all subsequent analyses (Fig. 1; Table S1).

Environmental variables

This study, like previous studies, employed bioclimatic and topographic variables to forecast species distribution (Malahlela et al., 2019; Nzei et al., 2021). Bioclimatic variables reflect annual trends, seasonality, and extremes in climate conditions and play an essential role in defining species' eco-physiological tolerances. Nineteen bioclimatic variables with a spatial resolution of 2.5 arc min were obtained from the WorldClim v2.1 (Fick & Hijmans, 2017) and integrated into our data (Table S2). We removed four

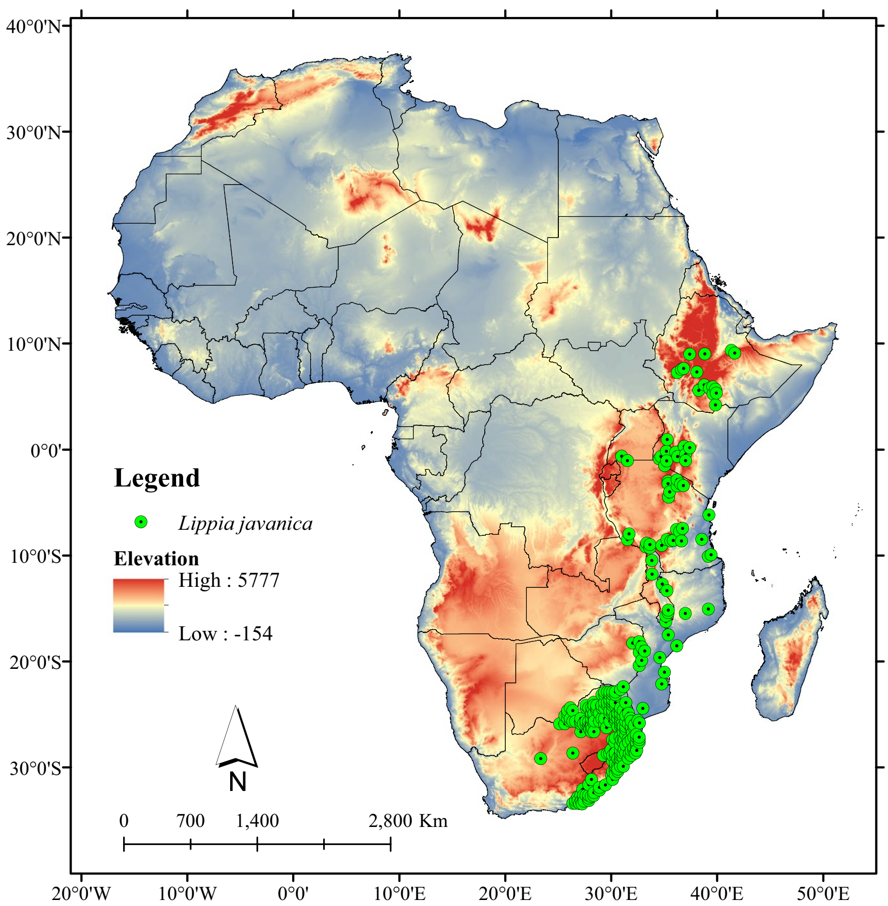

Fig. 1 Spatial distribution of *Lippia javanica* occurrence records based on the GBIF dataset plotted against the elevation distribution in Africa and Madagascar. Green dotted circles depict spatially unique occurrence records in the distributional range

data layers (Bio8, Bio9, Bio18, and Bio19) because they contained anomalies (Bede-Fazekas & Somodi, 2020). To minimize inter-variable correlation, we performed variance inflation factor analysis (VIF-step = 10) using the "*usdm*" package in R (Feng et al., 2019). The elevation variable, linked to climate and soil variables, potentially altering species composition, was obtained from the WorldClim2.1 database (Fick & Hijmans, 2017).

To simulate the potential distribution of *L. javanica* in Africa, three shared socio-economic pathways (SSPs) of the CMIP6 scenarios were considered. The SSPs complement the RCPs, which are pathways outlining greenhouse gas concentration scenarios, and consider the potential changes in socio-economic factors over the next century. They consist of the following: SSP1–2.6, characterized as "Sustainability – choosing the environmentally friendly path," envisions a world with a strong focus on sustainable growth and equality, resulting in low greenhouse gas emissions and an estimated long-term temperature increase of approximately 1.7–1.8 degrees Celsius. SSP2–4.5, titled "middle of the road," is an intermediate emission scenario with intermediate greenhouse gas emissions and CO_2 emissions remaining around current levels until the middle of the century. Lastly, SSP5–8.5, known as "Fossil-fueled development – following the high-energy route," presents a catastrophic scenario where the world experiences rapid economic growth and energy consumption, resulting in high greenhouse gas emissions and a long-term temperature increase estimated to be around 5.1 degrees Celsius (Riahi et al., 2017). These simulations were considered from the Community Climate System Model version 4 (CCSM4), for the 2050s (2041–2060) and 2090s (2080–2100), as it has been reported to produce good results for the African region (Nzei et al., 2021). For this study, we obtained the data for SSP1–2.6, SSP2–4.5, and SSP5–8.5 climate scenarios corresponding to the CCSM4 model. This dataset was obtained from WorldClim2.1 (Fick & Hijmans, 2017). All the climate variables had a spatial resolution of 2.5 arc mins.

SDMs modelling procedure and evaluation

We used Maxent version 3.4.3, which is a machine learning algorithm used to model the distribution of species based on data indicating their presence and various environmental factors (Elith et al., 2011; Phillips & Dudík, 2008). MaxEnt is known for its consistently strong performance compared to other available algorithms and is a widely employed tool for modeling species distributions, even when dealing with very limited data sets containing fewer than 100 observations (e.g., Ngarega et al., 2022). However, it is important to note that the effectiveness of MaxEnt can be influenced by the selection of modeling parameters, leading to issues such as model over-fitting, multicollinearity, and reduced prediction accuracy when using an excessive number of environmental layers (Merow et al., 2013). To address these statistical challenges, a model selection procedure was implemented based on established guidelines found in the works of Merow et al. (2013).

For model cross-validation, we used 30% of the occurrence data as test and 70% for training and replicated the models 20 times. The predicted area represents the "suitable space" that is suitable to be occupied by the species being modelled (Barve et al., 2011). The predicted space may exceed the observed occupied space due to various factors, including competition, dispersal barriers, or anthropogenic-enforced habitat loss. Like previous studies, we employed 10,000 random background points (Nzei et al., 2021; Mkala et al., 2022). We employed the area under the curve of the receiver operating characteristics curves and the True Skill Statistics (TSS = sensitivity + specificity—1,) to assess the model results (Phillips & Dudík, 2008; Allouche et al. 2006). The following criteria was used to assess the accuracy of the resultant models: poor performance (AUC 0.5), fair performance (AUC 0.5—0.7), and excellent (AUC > 0.7) (Parveen et al., 2022; Phillips & Dudík, 2008). We employed the 10th percentile as the training presence threshold value for creating boundaries that delineate areas suitable for the species. This specific threshold is believed to yield more ecologically meaningful results compared to more stringent threshold values, as suggested by Phillips and Dudík (2008).

Changes in habitat suitability

We calculated the area (in km^2) across the projection area and examined the changes between the baseline (current) and future scenarios in ArcGIS v.10.5 using the SDMtools v.2.5 extensions (Brown et al., 2017). The resulting output maps were utilized to visualize range shifts in three categories: (1) loss of suitable area, (2) gain of suitable area, and (3) stable range. ArcGIS v.10.5 was used for all analysis and visualizations.

Results

Model performance variable importance

Six of the 16 initial predictor variables were retained and integrated into the final model used to predict suitable ranges of *Lippia javanica* (Table S2 and S3). These six variables — Bio3, Bio4, Bio5, Bio12, Bio15, and elevation — had a relative importance on the distribution of *L. javanica* in Africa (Table 1). The predicted habitat suitability model performed exceptionally well for *L. javanica* as explored using average AUC and TSS of 0.953 and 0.826, respectively. Maximum temperature of the warmest month (Bio5), temperature seasonality (Bio4), and annual precipitation (Bio12) were the top three influential variables shaping the predicted spatial distribution of *L. javanica* by contributing 46.9%, 30.7%, and 10.1%, of total contribution values, respectively, based on correlation metrics (Table 1; Fig. S1). Based on the permutation importance, Bio5, Bio4, and Bio12 had the most powerful influence on the *L. javanica* model, with permutation importance values of 49.2%, 30.2%, and 8.0%, respectively. With 1.4% and 3.4% percent introduction and permutation importance, respectively, elevation (elev) contributed the least to the *L. javanica* distribution model.

Table 1 Relative importance (%) of environmental variables employed in developing the final habitat suitability model based on correlation and AUC metrics

Variable	% permutation contribution	Permutation importance
Bio5	46.9	49.2
Bio4	30.7	30.2
Bio12	10.1	8.0
Bio15	7.3	5.3
Bio3	3.5	3.9
elev	1.4	3.4

Habitat suitability responses to environmental variables

The response curves depicted the quantitative correlation between the logistic probability of the *L. javanica*'s occurrence and the six environmental variables, increasing our understanding of the ecological niche of this species (Fig. S1). According to the curves, *L. javanica* was observed to thrive at altitudes ranging from 400 to 3500 m. In addition, the optimal annual mean precipitation (Bio12) for the species growth ranged from 500 to 1500 mm, indicating a preference for average rainfall. The optimal isothermality (Bio3), determined by the ratio of Bio2 to Bio7 and reflecting regional temperature fluctuation, was approximately 50. Higher temperature seasonality, represented by Bio4, indicating the degree of temperature variation, showed that the highest probability of *L. javanica's* occurrence occurred in areas with temperature seasonality values ranging from 3000 to 4200. The maximum temperature of the warmest month (Bio5) values ranged between 220 and 260, which significantly influenced the distribution of *L. javanica*.

Current and future predicted distribution

The current projected range of *L. javanica* covers various regions in southern Africa, including Zimbabwe, South Africa, and Mozambique (Fig. 2), besides areas located in the Great Rift Valley covering Kenya, Ethiopia, Rwanda, Burundi, and Tanzania. Highly suitable areas were also found in Madagascar, where this species has not been recorded until now. In total, *L. javanica* had a predicted potential range of 2,11,8457.0 km^2 under current climatic conditions (Table S4).

Models predicting the future ranges using alternative climate models shared the trend of some range shifts by gain and loss of some parts of the project occupation space under the current climatic conditions. Under the future climates, all the SSP scenarios had an overall gain of suitable areas, except for the SSP–8.5 in the 2090s (Table 2; Figs. 3 and 4). In addition, the SSP scenarios in the 2050s had an overall lower change in suitable areas compared to the scenarios in the 2090s Table 2.

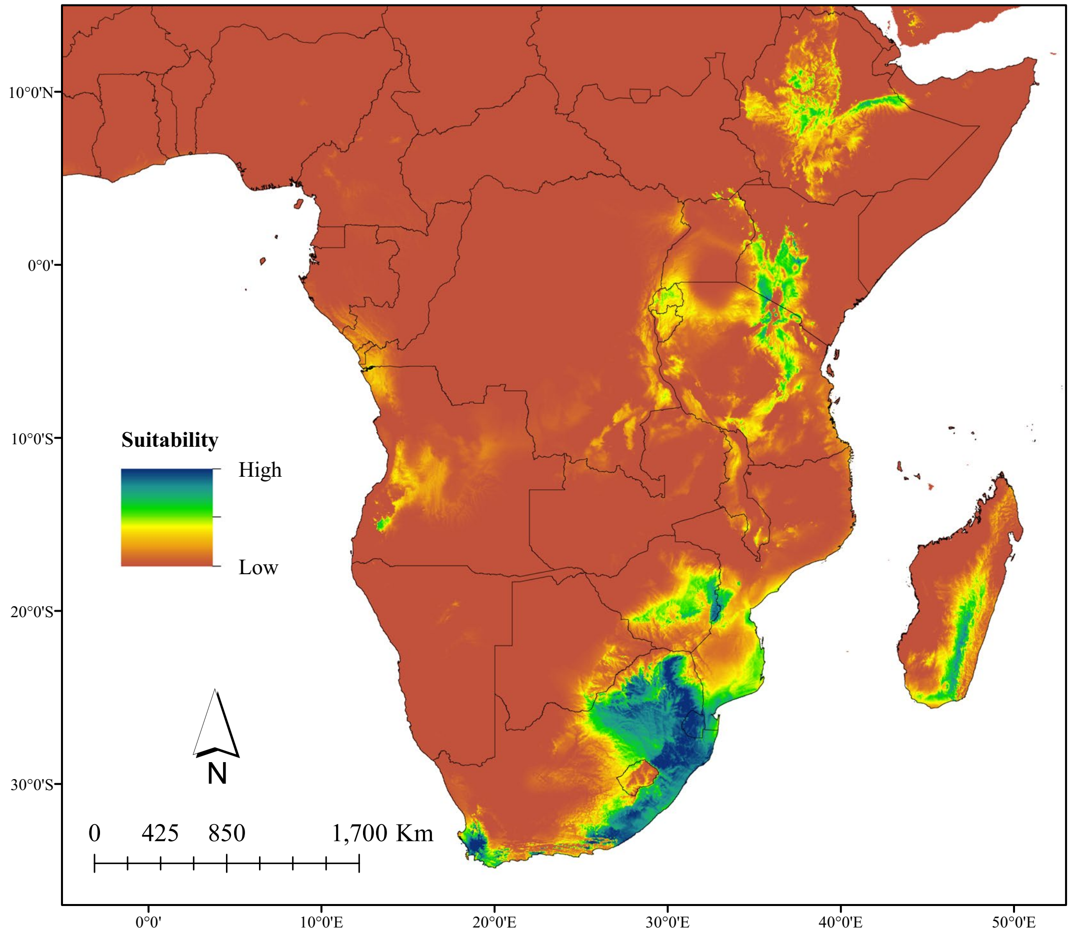

Fig. 2 Predicted climatic suitability for *Lippia javanica* under the current climate

Table 2 Changes in suitable areas in Africa for *L. javanica* under future climate scenarios

	Δ% SSP1–2.6	Δ% SSP2–4.5	Δ% SSP5–8.5
2050s	4.0%	2.88%	9.53%
2090s	45.97%	34.76%	-4.37%

Discussion

The greatly heightened species habitat loss rates due to climate change remain a concern (IPBES, 2019). Yet, relationships between environmental variables and the vulnerability risks of species remain largely unexplored. Moreover, the habitat of a species is critical for population development, reproduction, and survival, and its quality may directly alter species distribution and abundance (Mayor et al., 2009; Zhu et al., 2020). To the best of our knowledge, this is the first study to employ distributional modelling to forecast *L. javanica* potential distribution in Africa under current and future climate scenarios. The MaxEnt models performed exceptionally well, with an average AUC and TSS of 0.953 and 0.826, respectively. Our findings on *L. javanica* projected distribution were consistent with that of Van Wyk et al. (2008), who demonstrated that the species has an extensive distribution across tropical and subtropical regions of East and Southern Africa.

Temperature is critical for the germination, growth, and reproduction of *L. javanica.* The maximum temperature of the warmest month (Bio5) and temperature seasonality (Bio4) were two of the influential environmental variables influencing the distribution

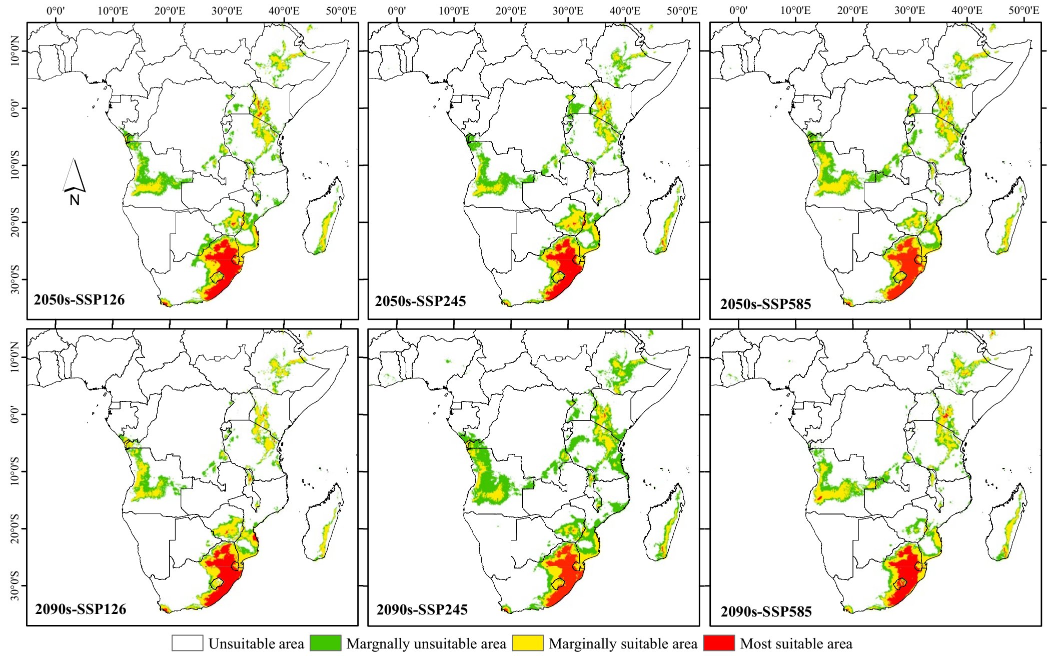

Fig. 3 Predicted climatic suitability for *Lippia javanica* in the 2050s and 2090s utilizing three distinct scenarios: SSP1–2.6, SSP2–4.5, and SSP5–8.5. Only tropical to southern Africa and Madagascar were depicted

of *L. javanica*. High temperatures during the warmest month can significantly impact the physiological and reproductive processes of many species, influencing their ability to survive and reproduce (Addo-Bediako et al., 2000). *Lippia javanica* mainly propagates through the seed, and the optimum temperature for germination is crucial to its growth or regeneration. Mattana et al. (2017) observed that *L. javanica* seed germination began at 15°C before peaking at 25°C, and seed germination declined when temperatures rose beyond 25°C. Mpati (2007), on the other hand, recorded that germination percentages of *L. javanica* increased at a constant temperature between 20 and 30°C. Additionally, temperature seasonality, which reflects the variation in temperature throughout the year, could have profound effects on the life cycles of species, affecting their phenology and behaviors (Root et al., 2003). Galíndez et al. (2017) investigated temperature impacts on seed germination of various *Lippia* species; the study found that the studied species germinated at shallow base temperatures, as low as 2.6 °C and 7.6 °C for *L. graveolens* and *L. javanica*, respectively. Therefore, differences in germination temperatures recorded by Mattana et al. (2017) and Galíndez et al. (2017) for *L. javanica* may illustrate the species' specific ecological adaptations to distinct climates. These findings underscore the importance of considering temperature-related variables in predictive modeling of species distributions and highlight the need for comprehensive assessments of climate-related factors in ecological research.

Current potential distribution results revealed that *L. javanica's* potential distribution area is mainly focused in the southern, east, and central African regions. The potential range of this species correlated best with the recorded localities of the species. Furthermore, the study's prediction findings will likely give potential localities for *L. javanica's* persistence and distribution and field surveys. *L. javanica* is known to grow well in high-altitude areas; this is in line with Madzimure et al. (2011), who reported that *L. javanica* is dominant in the hillside grasslands of Zimbabwe. Morgenthal et al. (2006), in their study conducted in South Africa, found that *L. javanica* predominantly occurs at higher altitudes. It is also known to thrive in diverse habitats, as reported by Ng'weno et al. (2010), who observed that the species also occur on forest margins, bush, and open grassland. The MaxEnt model predicted that the future distribution of *L. javanica* cuts across diverse habitats

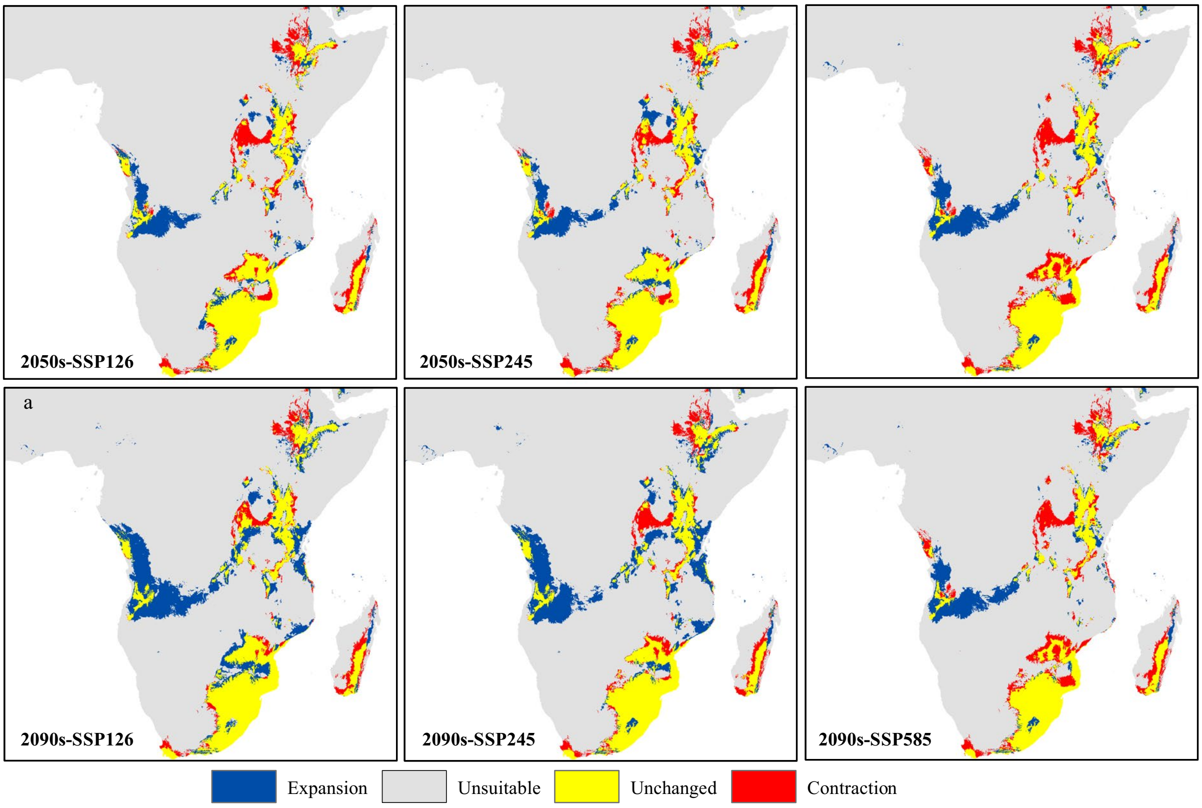

Fig. 4 Projected changes in the climatically suitable habitats of *Lippia javanica* for the 2050s and 2090s under SSP1–2.6, SSP2–4.5, and SSP5–8.5 scenarios. Only tropical to southern Africa and Madagascar were depicted

showing how highly adaptable it is in the face of climate change.

Climatic change significantly impacts Earth's biodiversity, including modifying seasonal phenologies and altering species' geographic ranges, community assembly, and extinction rates (Bellard et al., 2012; Zhao et al., 2018). According to future predictions, the potential habitat ranges will shift to higher elevations (Figs. 3 and 4). Future predictions also indicate that the distribution centers of *L. javanica* will remain in South Africa, East Africa, and Madagascar in 2050, albeit no significant reductions in suitable regions in the lower elevation limits of the distribution ranges (Table 2; Figs. 3 and 4). The predicted increase in habitat suitability ranges could provide important insights into the potential areas for the species to expand as shown in Fig. 4. Specifically, under the future scenarios in the 2090s (SSP1–2.6 and SSP2–4.5), the species are observed to increase, which is consistent with previous studies that species will move to higher altitudes (Thuiller et al., 2005). The regions may serve as potential conservation regions for the species management, particularly when the species is faced by potential threats. In addition, movement of species to higher areas is accompanied by higher rainfall patterns which foster the persistence of plant species. As a result, these high-suitability zones may continue serving as refugia by buffering localized climatic change. Previous research suggested that climate change would continue to drive species to higher elevations (Ngarega et al., 2022; Thuiller et al., 2005). As such, highly suitable areas in the future could be critical to preserving biodiversity, making it vital for biodiversity conservation efforts to locate future highly suitable regions (Nzei et al., 2021; Parveen et al., 2022). On the other hand, the observed reducing/lost areas could be posing a potential risk of species extinction by habitat loss in the future (Urban, 2015). All in all, plant species with large habitat niche will be better adapted to global climate change adaptation compared to plants with restricted niches (Khanum et al., 2013; Parveen et al., 2022).

Even though the analytical approach used in the current study is pertinent to various traditional plant species, we noted areas for improvement and resolved these concerns for future attempts. Firstly, despite *L. javanica's* documented distribution across Africa, the occurrence records obtained from the GBIF database were clumped in various regions (e.g., South Africa). While this study clarified this concern to a certain degree through an inquiry from various herbaria as well as publications, future SDM studies could also consider utilizing occurrence data (e.g., from published checklists and local herbaria) from data-scarce zones to typify climatic niches and ascertain potential distribution plant species utilized for traditional practices. Secondly, in this study, we used one global circulation model (GCM) and three shared socio-economic pathways (SSPs) to model the distribution of *L. javanica* under a climate change context. Given the distinct response of *L. javanica* to future climate conditions and the wide variability in temperature and precipitation patterns across the three SSP scenarios for the African region, it would be fascinating to investigate the species' responses across an array of SSPs and more representative GCMs.

Finally, the distribution of a species may be influenced by climate and topographic variables, anthropogenic disturbance, land-use change, edaphic factors, and several other social variables. In certain circumstances, due to the effect of microclimates, areas projected to be of low to medium suitability are essentially the potential distribution ranges of *L. javanica*. As a result, the outcomes of our study are just informative and need to be treated cautiously.

Conclusion

We projected the potential distribution range for *Lippia javanica* in Tropical Africa using maximum entropy modeling approach. The study results revealed the potential climate change effects on the distribution and abundance of the species in tropical Africa, as well as the vulnerability of plant species in the region. Given the ongoing increase in global surface temperatures, primarily fueled by human actions, it is crucial to adopt strategies that safeguard the natural habitats of indigenous species. Our results underscore the importance of the development of protective conservation measures to protect local biodiversity in various tropical African regions.

Acknowledgements We thank Elijah Mbandi Mkala for his assistance in statistical analyses. We also thank the anonymous reviewers for their helpful comments and suggestions.

Author contributions Boniface K. Ngarega conceived and designed the experiments, analyzed, and interpreted the results, and authored and reviewed drafts of the manuscript. Paul Chaibva performed statistical analysis, analyzed and interpreted the results, and authored the manuscript. Valerie F. Masocha performed statistical analysis, and analyzed and interpreted the results. Josphat K. Saina analyzed and interpreted the results and reviewed the drafts of the manuscript. Phyo K. Khine analyzed and interpreted the results and reviewed the drafts of the manuscript. Harald Schneider reviewed the drafts of the manuscript. All authors have read and approved the manuscript.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

Declarations

Competing interests The authors declare no competing interests.

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